

云南禄丰晚中新世的大熊猫祖先化石

邱占祥 祁国琴

(中国科学院古脊椎动物与古人类研究所)

关键词 禄丰 晚中新世 大熊猫

内 容 提 要

本文对 1981 年以前和 1983 年在云南禄丰古猿产地发现的,为本文后一作者于 1984 年和 1985 年订为 *Ursavus depereti* 的化石材料进行了再研究。通过对标本的仔细观察及与有关属种的对比,作者将上述化石材料订为一新属新种 *Ailurarcos lufengensis* gen. et sp. nov.。此种动物在形态特征和系统关系上介于 *Ursavus* 和 *Ailuropoda* 之间,它很可能代表了目前已知大熊猫类最早的祖先类型。

大熊猫 (*Ailuropoda melanoleuca*) 在外部形态和内部器官构造上既有熊科也有浣熊科的特征。关于它的起源及分类地位,从 1869 年订名以来,一直是学术界激烈争论的问题(详见朱靖, 1974),至今尚无定论。究其原因,除现生大熊猫本身形态和构造的独特性外,恐怕最主要的还是缺乏化石依据。就目前所知,最早的可靠化石记录仅限于华南巨猿动物群形成的初期¹⁾,其时代被笼统地称为更新世初期,而且从一开始出现就已是大熊猫属了(裴文中, 1974、1987)。虽然有许多全北区的中、上新世动物如 *Indarctos*、*Agriotherium*、*Ursavus*、*Arctotherium*、*Agriarctos* 等,都曾被看做是与大熊猫有较直接的系统关系,但它们或者因仅有极少的共同特征而被摒弃,或者因化石本身过于贫乏而难以令人信服。因此,时代较早的、公认可以归入大熊猫这一支系的化石迄今仍没有找到。这是目前在大熊猫起源和分类地位研究方面进展甚微的主要原因。

1981 年以前和 1983 年在云南禄丰古猿产地采集的熊科化石,已由本文后一作者分别于 1984 和 1985 年做过简要报道(祁国琴, 1984、1985)。对上述材料进一步研究后,我们认为,其中被订为 *Ursavus depereti* 的化石,很可能是目前已知最早的大熊猫类的代表。这一发现,对于解决长期争论的大熊猫的起源及分类地位等问题将会起到重要的作用。

一、标本记述

食肉目 *Carnivora* Bowdich, 1821

熊超科 *Ursoidea* Hay, 1930

1) 据黄万波同志告知,最近在云南元谋据称是上新世的地层中也发现了大熊猫类的化石。

大熊猫科 Ailuropodidae Pocock, 1929

始猫熊属 *Ailurarctos* gen. nov.

属型种 *Ailurarctos lufengensis* sp. nov.

特征 同属型种。

禄丰始猫熊 *Ailurarctos lufengensis* sp. nov.

1984 *Ursavus depereti*: 祁国琴 pp. 53—61; pl.

1985 *Ursavus depereti*: 祁国琴 pp. 33—43.

(图版 I, 1—6; 图 I, 1; 图 2, 1)

正型 左 P^4 (V. 6892. 12), 产自第二层(见吴汝康等, 1982)。

众型 第二层: 左 P_4 (V. 6892. 13); 左 M_3 (V. 6892. 11)。第三层: 右 P^4 (V. 6892. 1), 前尖破损、后附尖缺失(原订 DP^4); 右 M^1 (V. 6892. 2), 前缘破损; 左 M^1 (V. 6892. 3), 前尖及次尖基部破损; 右 M^2 (V. 6892. 4), 只保存跟座部分; 左 M^2 (V. 6892. 5); 右 M^2 (V. 6892. 6); 左 P^2 和左 P^3 (V. 6892. 7) (原订右 P_3 和右 P_4); 左 P^4 (V. 6892. 8), 只保存前附尖和前尖(原订右 P_4); 右 M_1 (V. 6892. 9), 只保存三角座部分; 右 M_2 和右 M_3 (V. 6892. 10)。第五层: 右 M^2 (V. 6892. 14)。

特征 一种形态原始、个体大的大熊猫类动物。其颊齿齿列长约为现生大熊猫的三分之二。前臼齿形态与大熊猫者相似, 而臼齿形态则与 *Ursavus* 更接近。 P^2 双根, 前附尖极小, 不与 P^3 呈覆瓦状叠接。 P^3 双根、三尖, 舌侧基部附属小尖很小, 尖间无中凹。 P^4 基本形态与大熊猫者同: 三根、三个接近等大的唇侧尖, 三个舌侧基部的小尖, 在“原尖”¹⁾和“次尖”之间有一极小的尖, 但比例上更宽短, “次尖”不再分出附属小尖, 外齿带发育明显。 M^1 长稍大于宽, 无原小尖和后小尖。原尖和次尖嵴形, 中间以凹槽分开。齿带发育弱, 舌侧向后仅达次尖中部。 M^2 比 M^1 稍长, 跟座与三角座大小相近, 跟座呈圆形凹面, 三角座近一梯形。 P_4 两根、三尖, 舌侧基部后端内隆。 M_1 三角座短粗, 下前尖前缘倾斜很缓, 下后尖距下原尖远, 位置较靠前, 下原尖后壁基部有一附属尖。 M_2 舌侧明显高于唇侧, 下前尖尚可辨认出。 M_3 圆小。颊齿, 特别是臼齿的冠面布满深的褶皱。

地质时代 晚中新世, 距今 7—8 百万年(详见 Flynn L. et Qi, 1982)。

描述 全部材料共 16 颗牙齿, 其中 6 颗是不完整的。产自第三层的最多, 共 12 颗。有趣的是, 除 M^2 有 3 颗 (V. 6892. 4, 5, 6) 外, 其余的牙齿没有重份的。经过仔细观察可以判定 V. 6892. 5 (左 M^2) 和 V. 6892. 4 (右 M^2) 是左右对称的, 而 V. 6892. 6 则是属于另一个体。这一事实加上这些牙齿的保存状况相同, 磨蚀都很轻微, 而且都具有极发达的珐琅质褶皱, 确使我们相信第三层的牙齿, 除 V. 6892. 6 外, 极可能是属于同一个体的。

P^2 齿根断失, P^3 尚保留前根的半段, 两者舌侧基部珐琅质都稍有破损。这两个牙齿形态相近, 都是一面隆凸, 一面较平, 较平的一面基部有齿带不规则隆起。这种形态和大熊猫的上前臼齿以及下面要记述的 P^4 都是一致的, 因此它们应该是上前臼齿而不是

1) 按照大多数古生物学家的意见, 此处“次尖”应为原尖, 而“原尖”应由齿带膨大而成的一个附属小尖——见后。

下前臼齿。此外,它们都是双根、三尖,这又排除了它们是 P^1 (单根、单尖)和 P^4 的可能,所以只能是 P^2 和 P^3 (原鉴定为 P_2 和 P_3 ,在 1984 年的图版 I, 1c 中它们的前、后方向也是反的)。从牙齿冠面看,它们都是两端略尖的椭圆形,一条纵嵴贯穿整个齿冠的顶部。牙齿的三个尖都比较侧扁、锐利。 P^2 的前附尖很小,稍向前内方歪曲。后附尖比前附尖大,但明显地比 P^3 的前附尖小。附尖与主尖间均以切迹分开。主尖远大于附尖,其舌侧面正中有棱状突起,突起的前后方各有一条弱沟把它和前、后的平面分开。唇侧齿带不明显,舌侧呈瘤状。牙齿的前、后端无任何与相邻牙齿接触而形成的压迹。 P^3 在形态上与 P^2 接近,但更大。前、后附尖在比例上也大,与主尖分离得更加明显。唇、舌侧均具齿带,但舌侧者更清楚。舌侧基部珐琅质破损,从保留的齿质部分可以看出,在主尖前半部处有一小突起,突起之后稍稍凹陷,然后又有一向舌侧方向的突起。

P^4 唇侧三个尖(前附尖、前尖和后附尖)形态几乎一样,都是外凸内平。前尖和后附尖也不形成裂叶,前尖只比其它两尖稍高大,前附尖是其中最小的。在 V. 6892. 12 的舌侧可以看到三个尖:原尖最大,位于前尖后端水平,它之前有一很小的附尖,再前又为一较大之附尖。中间的小附尖位于原尖和前面附尖之间的谷部。唇侧齿带发育,舌侧齿带在前、后端都较明显,向中间延伸至三个舌侧尖的顶部。因此这三个尖可以看成是由齿带扩大升高而形成的。整个齿冠都布满细的褶皱,在唇侧和舌侧尖的舌面上褶皱更粗大些。牙齿三根,内根在原尖和它前面的小附尖之下。此根基部另有一细小分枝倾伸向前内方。舌侧最前边的附尖没有根支持,它部分地座落在前根之上,前根较粗大,但仍比后根细小些。

V. 6892. 1 原被看做是 DP^4 (祁国琴,1984,图版 I, 1a)。其前尖外后部破损,后附尖完全缺失。前附尖和前尖保留的部分无论在形态还是大小上都和上述的 P^4 者相同,和臼齿者差别很大,所以也应该是 P^4 。然而它的舌侧构造与 V. 6892. 12 确有些不同:首先是它最前边的附尖小,和中间的附尖差不多大;其次是牙齿舌侧向内最突出的地方不是在原尖的前端,而是在中间附尖处,这使牙齿的舌面形成一圆弧形而不像在 V. 6892. 12 中那样成两面角形。这些不同目前只能看做个体变异。

M^1 有两颗,但都不完整。长方形、长稍大于宽。前尖和后尖呈锥形,相当高耸。后尖舌面中央为棱嵴状,两侧各以弱沟与舌面的其它部分分开。无后附尖。原尖为 L 形嵴状,其纵向部分高耸,其舌面几近陡直。次尖 (Schlosser 认为这应为后小尖) 更近锥状,它和原尖后嵴以一切迹分开。次尖唇面中央较高,与后尖舌面中棱形成一屋嵴状隆起。由四个主尖围绕而成的中央凹相当深,最深处位于前、后尖舌面之间。分隔原尖和次尖的切迹以一弯曲的沟和中央凹最深处相通。外齿带不发育,内齿带前端伸达牙齿前缘,其后端向后稍稍升高止于次尖最高处。整个牙齿冠面都有十分发育的褶皱,在原尖和次尖的唇面上最为粗壮,而在牙齿四周较弱。

M^2 的前尖与 M^1 的不同,它的舌面不但有一条中央棱嵴,其前还有一条稍短的棱,两棱间以沟相隔。后尖较前尖低小,它的舌面棱嵴更尖削,斜向前内方,与原尖嵴连在一起,使整个三角座成为一个由嵴所封闭的梯形。次尖为锥形,跟座面积稍小于三角座,冠面斜向外后方。齿带仅在舌面原尖和次尖之间发育。整个冠面上都有极发育的褶皱。三角座上的褶皱较细长,呈平行分布,跟座上的褶皱较短,呈不规则状。在 V. 6892. 6 标本上,在后尖前嵴的舌侧前端还有一沟,此沟使后尖的前端似乎又分隔出一个小尖来(此小

尖在太熊猫中有)。它的次尖的嵴也更发育:一条斜向前外方,几乎伸达后尖与原尖的连嵴;一条较短的伸向前方,几乎和原尖后嵴相连;一条则向后形成跟座的周缘嵴。

P_1 具两根三尖。三个尖的形态和大小均相近。主尖(下原尖)最大,前边的尖(下前尖)最小。三个齿尖都侧扁,一条纵嵴贯穿三个尖的顶部。牙尖舌面隆凸,唇面较平坦,和上前臼齿不同的是瘤状的齿带在舌面。这些正是大熊猫下前臼齿的特征。下原尖隆凸的一面(舌面)有明显的中央棱嵴并伴以两侧的浅沟。其它两尖舌面的中嵴表现较弱。外齿带在前端隐约可见,在下后尖外侧表现清楚。内齿带贯穿全长,而以后半部最明显。在下原尖舌面中嵴基部有一附加小嵴,牙齿的后内角处也呈小瘤状。因此从冠面看,牙齿的后端最宽,齿冠表面有细弱的皱纹。

M_1 仅保存一三角座。三个尖都很粗矮。下前尖为短嵴形,斜向后外方,但仍与下原尖前嵴组成平滑弧形。下前尖的前缘不陡直,相当平缓地斜向前下方,它的外壁平,内壁隆凸。下原尖外壁陡直,看不见牙齿前外角向外扩展的迹象。内壁圆隆,也有中棱嵴及其两侧的弱沟。自下原尖顶向内后方伸出一嵴。下原尖后壁还有一附加的瘤状突起。下后尖是三个尖中最低的,但也相当粗壮。它的位置较靠前、距下原尖较远,中间以一切迹相隔。

M_2 近长方形,前端稍宽于后端,整个牙齿咀嚼面由相当尖削的嵴所封闭。舌侧显著地高于唇侧,唇侧面较平但向外侧方倾斜,舌侧面较圆隆。下前尖仍可辨出,位于牙齿的前内角。下后尖位置稍稍偏后。下原尖和下后尖以嵴相连。此嵴距外侧三分之一处向前伸出一粗短的隆起但不达牙齿前缘。自下原尖后嵴长二分之一处向内后方也伸出一个相当明显的嵴,它与自次尖向前内方伸出的嵴交会,构成与“上猿三角”相似的构造。下次尖与下原尖之间以明显的切迹分开。下后尖是 M_2 中最高大的尖。下内尖呈嵴状,不太明显地分为前后两个尖。无齿带。咀嚼面和唇侧面有很强的褶皱。

M_3 接近圆形,前后径稍大于宽。下原尖为三条斜伸向后内方的粗嵴,其外壁特别倾斜。牙齿周围的嵴不及 M_2 的明显,冠面边缘处的褶皱呈向心状伸向牙齿中心。

二、与有关属种的比较

上述材料虽然是采自同一地点的很小范围内,但无上、下颌骨,只有零散的牙齿。我们必须首先解答:为什么把上述牙齿当作同一种看待。第一,这些牙齿在形态上具有明显的一致性。虽然是不同部位的牙齿,但不同程度地都具有从 *Ursavus* 向 *Ailuropoda* 过渡的特征。其中最鲜明的一点是,在所有牙齿上都有强烈发育的珐琅质褶皱,这一点很容易使它与禄丰古猿地点另一种大小相近的熊类化石区分开(关于后一种熊类化石将另文发表)。第二,这些牙齿在大小上可以相互匹配。最后,如前所述这些牙齿中的大多数都产自同一剖面的同一薄层(第三层),而且极有可能是属于同一个体的。基于上述理由,我们相信把它们归为同一个种是合理和可信的。

上述禄丰大熊猫类化石牙齿、特别是前臼齿在形态上的特殊构造,使我们很容易把它们和现知的浣熊和熊科的大部分成员区分开。在形态上可以和上述标本相比的只有 *Ursavus*、*Ailuropoda* 和 *Agriarctos*。

1. 和 *Ursavus* 的比较

Ursavus 是 M. Schlosser 1900 年创立的。目前所知已记述了九个种(亚洲一个, 欧洲六个, 北美两个), 时代从早中新世(欧洲 MN3)至晚中新世(相当欧洲的 MN12)。这九个种中的绝大多数在形态上都很一致, 只有发现于欧洲的 *Ursavus ehrenbergi* 和 *Ursavus depereti* 构造比较特殊, 我们将在稍后专门讨论。典型的 *Ursavus* 和禄丰标本有以下共同特征: (1) 前臼齿齿式全, 不互相紧靠。P²、P³ 和 P₂-P₄ 都有两个根, 禄丰材料中虽然没有 P₂ 和 P₃, 但根据其上前臼齿推测, 它们大概也是双根的。(2) P⁴ 是三根的。(3) 上、下臼齿的构造型式一致, 大小比例也相近。M¹ 接近方形或长稍大于宽, M² 跟座比三角座小, 整个牙齿和 M¹ 差不多长或稍长, M₂ 短于 M₁, M₃ 小而圆。以上这些特征不仅仅是 *Ursavus* 和上述禄丰标本之间的共同特征, 实际上不同程度地也存在于大多数熊科较早期的成员如 *Hemicyon*、*Indactos*、*Agriotherium* 中。在 *Ursus* 中则是不存在的。

禄丰标本和典型的 *Ursavus* 的区别也是很明显的。(1) 禄丰标本中所有前臼齿都是三尖的, P⁴ 及 P₄ 的三个尖几近等大, P⁴ 的前尖和后附尖已不再形成具切割作用的“裂叶”, 原尖位置后移。在 P₄ 和 P³ 以及 P⁴ 的舌侧基部均出现由齿带膨大形成的附属隆起。在典型的 *Ursavus* 中前臼齿(除 P⁴)都是单尖的, 前、后附尖即使有也很弱, P⁴ 无前附尖, 前尖高大, 与后附尖形成“裂叶”, 原尖前位, 前臼齿内侧基部无附属隆起。(2) 禄丰标本中唇侧齿带都发育很弱, 特别是在臼齿上。在典型的 *Ursavus* 中, 齿带相对较强, 特别表现在臼齿上。(3) 禄丰标本上都具有强烈发育的珐琅质褶皱。*Ursavus* 者一般也较发育, 但显著较弱。上述特征中, 第二点是进步熊类共有的特征, 而第一和第三点则只有在 *Ailuropoda* 中有。

Ursavus depereti 是 *Ursavus* 属中问题较多的一个种。它是 1902 年由 M. Schlosser 根据西德符腾堡州 Melchingen 裂隙堆积(可能为 Vallesian 期)中的一颗 M₁ 和一颗 M₂ 建立的。是这个属中个体最大的一个种。1928 年 Deperet 和 Lluca 记述的采自法国里昂东南 Luzinay (Vallesian 期)的一段带 M₁ 和 M₂ 的下颌在大小和形态上都和 Melchingen 的差不多, 大概可以归为一个种。问题出在 Viret 和 Mazenot 1948 年记述的采自里昂东北 Soblay 地点 (Vallesian 晚期) 的一批材料。这批材料包括 P⁴、M¹、M² 和 M₂。其中可以和 Melchigen 材料直接对比的只有 M₂。鉴于这颗牙齿和 Melchigen 的看不出有多大区别, Viret 和 Mazenot 把上面的牙齿也全归入了 *Ursavus depereti*。上臼齿和一般的 *Ursavus* 者没有多大差别, 但 P⁴(AA52 bis) 的形态十分特别: 它有一个很大的前附尖, 它的原尖由一个中沟分成前、后两个尖, 分别位于前尖的前、后部, 使 P⁴ 的轮廓变成一个正三角形。这种构造在 *Ursavus* 这个属中从未有过。Viret 和 Mazenot 对这个牙齿的归属很费了些脑筋。他们提出, 这个 P⁴ 可能和印度的 *Lydekkerion*(= *Agriotherium*) 的 P⁴ 最接近。不过最后他们还是倾向于把它看作 *Ursavus depereti* P⁴ 的个体变异。1949 年 Viret 在同一个地点又发现了新材料。其中有一块带有 P⁴ 和 M² 的上颌(AA96)。M² 和 1948 年记述的一样, P⁴ 则与 AA52bis 既相似又有区别: 它仍然有前附尖但明显较小; 它的原尖只有一个位于舌侧中央; 原尖之前还有一

个由齿带膨大而成的小尖。Viret 认为这证实了他关于这种动物 P^4 变异范围较大的推测,也更坚定了他把这些牙齿都归入 *Ursavus depereti* 的想法。1979 年 E. Thenius 首次指出, Soblay AA52 bis 这颗牙齿应属于大熊猫类,把它归入了 Kretzoi 1942 年订的一个当时地位还不清楚的属 *Agriarctos* (详见后)。通过对比我们发现, Soblay 的 P^4 虽然在外形上和禄丰的标本有些相似,但差别仍很大: (1) 在 Soblay 的两个 P^4 上后附尖都明显地长于前附尖,它的顶缘前后不对称,前缘很短,后缘较长且有一微凹,其唇面也有一中凹,这正是形成“裂叶”的后附尖的形态。在 AA96 标本上前附尖则更小。这和上述禄丰的三尖近于等大,“裂叶”消失的 P^4 是很不同的。(2) 在 Soblay 的两个 P^4 中,原尖退至舌侧中线附近、或者说舌侧最突出的部分位于中线附近,而在禄丰标本中原尖后位, P^4 轮廓为一尖角向后的不对称三角形。不管将来 Soblay 的 P^4 归入何属何种,有一点是肯定的,它们和禄丰标本的差别还是相当明显的。这种差别意味着裂齿功能的根本转变。我们认为这两者应该分属于不同的属。

2. 和 *Ailuropoda* 的比较

两者共同的特征是(1) P^2 、 P^3 和 P_4 (可能还有 P_2 、 P_3)都是双根三尖的。上牙唇侧圆凸,舌侧平;下牙相反,舌侧圆凸而唇侧平,但两者舌侧都有不同发育程度的小隆起。(2) 两者 P^4 的形态几乎完全一致:唇侧三尖大小及形态接近,外凸内平,没有“裂叶”,原尖后位,支持原尖的内根也相应后移,原尖前有一个很小的中间小尖,再前又有一大的前内附尖。(3) M^1 和 M^2 的珐琅质褶皱极为发育,外齿带极弱或无。(4) M_1 的三角座各个尖都较粗矮,下前尖内移,其前缘不垂直向下很平缓地斜向前下方,下后尖位置相当靠前,离下原尖远。(5) M_2 和 M_3 珐琅质褶皱极发育, M_2 分割三角座和跟座的横沟明显,下前尖尚可辨认,舌侧远高于唇侧。以上这些特征是除大熊猫外现知熊类中其他成员都没有的,可以认为是大熊猫这一特殊支系的自近裔性状。

禄丰标本和大熊猫属之间的不同有: (1) 禄丰标本的前臼齿大概不像大熊猫中那样互相紧靠,且 P^2 与 P^3 呈覆瓦状接触并斜向前内方,这点可从禄丰的前臼齿标本上未发现因相邻牙齿紧靠而形成压迹推断出来。(2) 禄丰标本中前臼齿各尖都相当侧扁,舌侧的附属小瘤多仅处于萌芽状态, P^4 舌侧尖也不再分为次级小尖。在大熊猫中前臼齿的尖都很粗胖,呈锥形,舌侧的附属尖在 P^2 、 P^3 和 P_4 中已很发育了。(3) 禄丰标本中 M^1 仍是长稍大于宽,内齿带不宽大,向后终止于次尖中部水平, M^2 的情况与 M^1 差不多,只是跟座后端总是很圆。在大熊猫中 M^1 总是宽大于长,有很发育的原尖和次尖,内齿带极宽并向后伸延至牙齿后缘, M^2 后端总是尖的。(4) M_1 在大熊猫中下后尖高于下原尖几乎与下原尖处于同一横线上,牙齿的前外角明显向外扩展,下后尖和下前尖的基部大大靠近以致相接。在禄丰标本中下后尖的位置仍较靠后并不高于下原尖,其基部离下前尖者还较远,牙齿前外角不见扩展的迹象。(5) M_2 在大熊猫中分割三角座和跟座的横沟特别明显,而且自冠面看此处唇侧有明显的收缩沟,此外围绕齿冠的嵴不尖锐。在禄丰标本中三角座和跟座分隔不明显,但齿冠周围的嵴却很尖锐。(6) M_3 在大熊猫中或为横宽的椭圆形或为三角形。在禄丰标本中它是近圆形的。(7) 在所有大熊猫的臼齿上都有极具特征的泡状纹饰,而在禄丰标本上大多为深而长的褶皱。从以上对比可以看出,大熊猫属

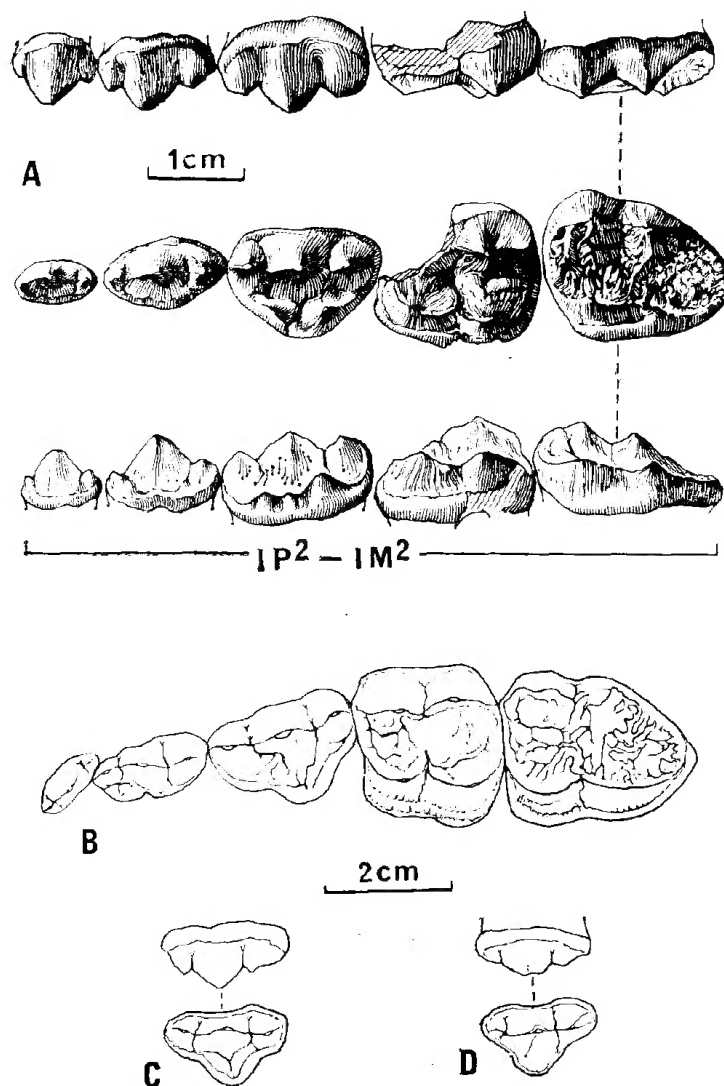


图1 大熊猫类及有关属种上颊齿的比较

Fig. 1 Comparison of upper cheek teeth of ailuropods with the related genera and species

A. 禄丰始猫熊 新属新种 *Ailurarctos lufengensis* gen. et sp. nov. 左 $P^2P^3(P^2P^3 \text{ sin.})$ V. 6892.7, 左 $P^4(P^4 \text{ sin.})$ V. 6892.12; 左 $M^1(M^1 \text{ sin.})$ V. 6892.3, 左 $M^2(M^2 \text{ sin.})$ V. 6892.

5. 唇面视 labial view, 冠面视 occlusal view, 舌面视 lingual view;

B. 大熊猫 *Ailuropoda melanoleuca* 左 $P^1-M^2(P^1-M^2 \text{ sin.})$ (Davis, 1964, Fig. 68 reversed), 冠面视 occlusal view;

C. “迪氏祖熊” “*Ursavus depereti*” 左 $P^4(P^4 \text{ sin.})$ Soblay AA 52 bis (Thenius, 1979 Fig. 2, E). 唇面视 labial view, 冠面视 occlusal view;

D. “迪氏祖熊” “*Ursavus depereti*” 左 $P^4(P^4 \text{ sin.})$ Soblay AA 96 (Viret, 1949 Fig. 1). 唇面视 labial view, 冠面视 occlusal view

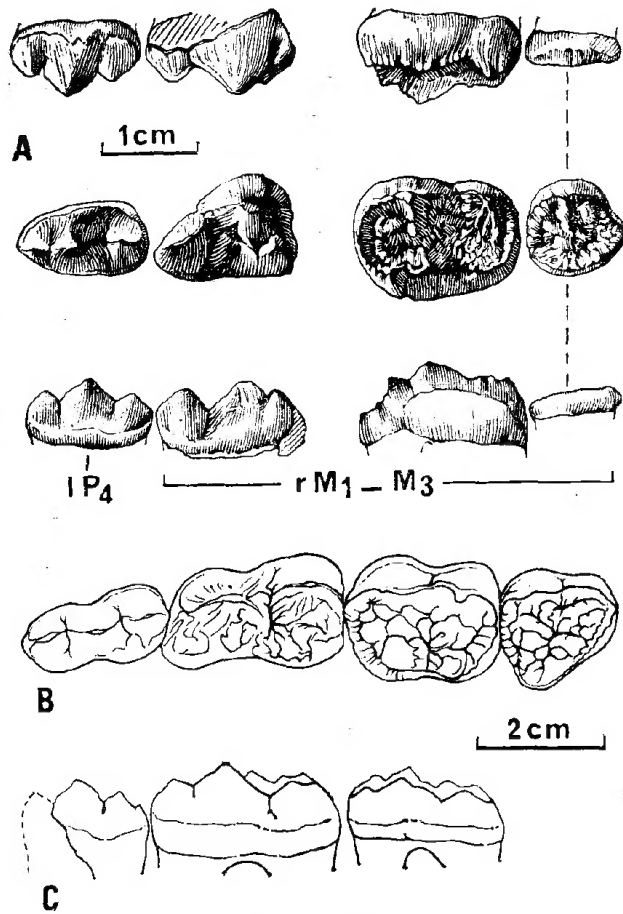


图2 大熊猫类及有关属种下颊齿的比较

Fig. 2 Comparison of lower cheek teeth of ailuropods with the related genera and species

- A. 禄丰始猫熊 新属新种 *Ailurarctos lufengensis* gen. et sp. nov. 左 P_4 (P_4 sin.) V. 6892. 13, 右 M_1 (M_1 dext.) V. 6892. 9, 右 M_2 、 M_3 (M_2 and M_3 dext.) V. 6892. 10. 唇面视 labial view, 冠面视 occlusal view, 舌面视 lingual view;
- B. 大熊猫 *Ailuropoda melanoleuca* 右 P_4 — M_3 (P_4 — M_3 dext.) (Davis, 1964 Fig. 68 reversed) 冠面视 occlusal view;
- C. 葛氏郊猫熊 *Agriarctos gaali* 左 P_4 — M_3 (P_3 — M_2 sin.) (Kretzoi, 1942 Fig. 1, 4 reversed) 唇面视 labial view

所具有而禄丰标本所不具有的特征,正是大熊猫这一支的近裔性状,是任何其他支系所不具备的。

3. 与 *Agriarctos* 的比较

这个属是 M. Kretzoi 1942 年根据匈牙利潘诺盆地发现的一些牙齿创立的。发现于 Hatvan 地点 (Turolian 偏晚期) 的有右 P_3 — M_2 (P_4 前半部破损); 发现于 Rozsasz-entmarton 地点 (Turolian 偏早期) 的只有一颗左 M_1 。根据 Kretzoi 的记述,这个属的

特征是: “一类中等大小的 *Agriotheriinae* (M_1 长 22—28mm), 牙齿粗壮, 下前臼齿具有较低的下原尖(主尖)和强壮的附尖, M_1 短宽, 下后尖粗壮, 位置前移, 因此下三角座三尖互相紧靠”。Kretzoi 在创立这个属时把 Schlosser 1902 年记述的 Melchigen 的 M_1 和 M_2 也归入了 *Agriarctos*, 因为它比匈牙利标本的尺寸小 (M_1 长为 22.5mm; 27.3—28.5 mm), 认为应是另一个种, 这样就把 Melchigen 的标本叫做 *Agriarctos depereti*。

Viret 和 Mazenot(1948) 对 Kretzoi 的 *Agriarctos* 颇不以为然, 他们认为这是一种前臼齿特化了的 *Indarctos*, 因而又恢复了 *Ursavus depereti* 的地位。Thenius(1979) 则把 Soblay 的一颗 P^4 (AA52 bis) 归入 Kretzoi 的 *Agriarctos*, 并把 *Agriarctos* 归入大熊猫类。

表 1 大熊猫类及有关属种牙齿测量和对比(单位: 毫米)

Table 1 Comparison of the teeth of ailuropods with the related genera and species in measurements (in mm)

		<i>Ailurarctos</i> <i>lufengensis</i>	<i>Ailuropoda</i> <i>microta</i> (Pei, 1987)	<i>Agriarctos</i> <i>gaali</i> (Kretzoi, 1942)	<i>Ursavus depereti</i> (Schlosser, 1902)	" <i>Ursavus depereti</i> " Soblay(Viret et Mazenot, 1948; Viret, 1949)
P^2	L	8.6				
	w	5.2				
P^3	L	12.2	15.5			
	w	7.4	8.2			
P^4	L	15.5	19.7—21.0			20.3(AA52 bis), 18.1(AA96) ¹⁾
	w	11.3	12.5—14.3			—14.0(AA52 bis) ¹⁾ , 12.2(AA96) ¹⁾
M^1	L	17.3	17.7—21.5			18.7
	w	~15.3 ~15.6	16.5—23.2			16.2
M^2	L	19.8 17.6	20.0—23.5			21.5
	w	14.9 14.2	16.3—19.5			16.0
P_4	L	13.9	16.2—19.1			
	w	7.9	9.5—11.0			
M_2	L	17.2	17.9—20.5	24.1	16.8	
	w	12.9	15.2—16.5	16.0	10.8	
M_3	L	10.7	11.1—13.7			
	w	9.4 9.6	12.5—15.8			

1) 根据图测量所得 (The measurements according to the Figs.)

匈牙利的 *Agriarctos* 标本记述得过于简单。Kretzoi 既没有提供照片, 也没有附以较好的插图, 因此其细微特征很难辨识。和禄丰的标本相比我们可以看出至少有以下相同之处: (1) 下前臼齿都是双根三尖。(2) M_1 三角座下前尖前缘不陡直, 下原尖相对较低, 下后尖不低于下前尖, 离下原尖远但位置相当靠前。(3) M_2 的构造也很相近, 似乎都

有分离的下前尖。但两者也有明显的不同：(1) 匈牙利标本个体显著地大，总体看来比禄丰者大三分之一或更多(见表 1)。(2) 匈牙利标本中的 M_2 可能相对较长。由于禄丰标本中只有 M_1 的三角座，我们将两者 M_2 的长度和 M_1 三角座的长度进行对比，匈牙利标本为 $24.1 (M_2 \text{ 长}) / 19.8 (M_1 \text{ 三角座长}) = 121.7$ ，禄丰标本为 $16.5 (M_2 \text{ 长}) / 15.5 (M_1 \text{ 三角座长}) = 106.4$ 。(3) 匈牙利标本中 M_2 舌侧嵴高于唇侧嵴的程度较低，它的下原尖仍相当高大，它与下次尖分隔的切迹比较靠前。(4) Kretzoi 既没有提到下前臼齿是否外平内凸(这在熊类中是极特殊的)，也没有提到褶皱的发育情况。我们相信，像 Kretzoi 这样有经验的古生物学家，如果这些特征确实存在的话是不会将它们忽略的。总之，匈牙利和禄丰标本之间确有许多不同之处。这些不同表明匈牙利标本在进化水平上较禄丰者稍高(个体大、 M_2 更长等)，但它并非沿着向 *Ailuropoda* 发展方向进化的。

Soblay 的 P^4 (AA 52 bis) 究竟应该归入 *Ursavus* 还是 *Agriarctos*，目前还很难断定。*Ursavus depereti* 和 *Agriarctos* 的正型标本中都没有上牙，它们之间无法直接进行比较。但根据我们的观察，这颗 P^4 仍然具有“裂叶”，这种情况在 Soblay 的另一件和 M^1 连在一起的 P^4 上也可以看到，在希腊优卑亚岛上发现的 *Ursavus ehrenbergi* (见 Ginsburg, 1982, Fig. 6) 中也可以看到。它们的前附尖都比 AA 52 bis 者更小，也具有“裂叶”。所以看来它们还都应被归入 *Ursavus* 这个属，代表了这个属中向大熊猫方向开始进化的一支。

三、几点结论

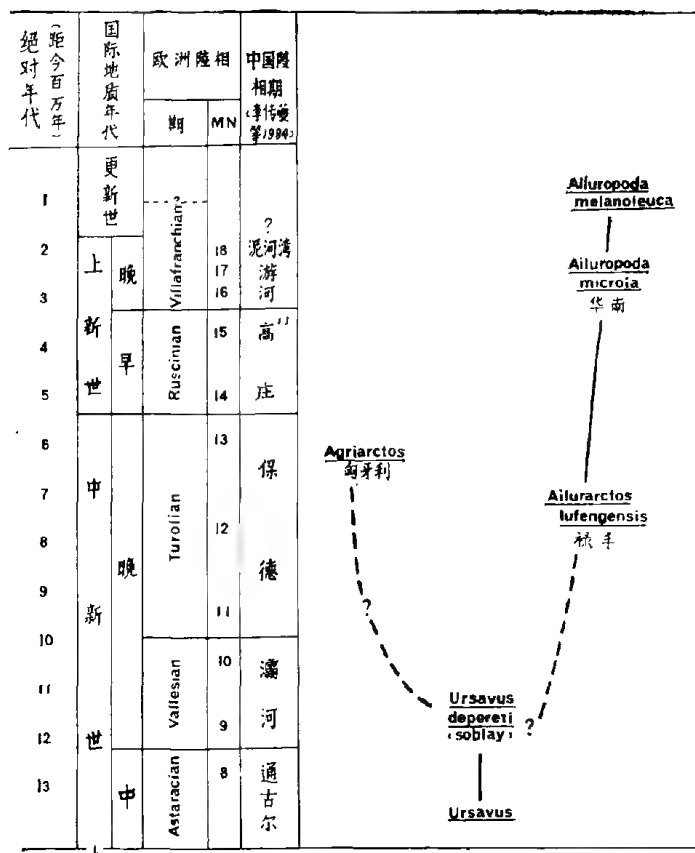
1. 禄丰的 *Ailurarctos* 和 *Ursavus* 的共同特征对于后期进步的熊类来说都是近祖性状；*Ailurarctos* 与 *Ursavus* 的不同则是前者的近裔性状。*Ailurarctos* 和 *Ailuropoda* 之间的共同特征中的绝大多数，对于熊类的其他代表来说都是这两个属所共有的自近裔性状，它们之间的不同则表明 *Ailurarctos* 尚不具备 *Ailuropoda* 所具备的某些自近裔性状。因此可以肯定 *Ailurarctos* 在形态和系统关系上介于 *Ursavus* 和 *Ailuropoda* 之间。

2. Soblay 的 *Ursavus depereti* 和希腊的 *Ursavus ehrenbergi* 在形态上、特别是在 P^4 的构造上，介于典型的 *Ursavus* 和 *Ailurarctos*-*Ailuropoda* 之间。从 P^4 的基本型式和功能考虑，它们具有“裂叶”，仍保留着肉食性切割作用，更接近于 *Ursavus* 一边。它们和 *Agriarctos* 的关系尚需进一步证实。

3. *Agriarctos* 正型标本已经具有大熊猫类的基本特征，而这是所有其他熊类所没有的。它的某些不同于 *Ailuropoda* 的进步特征，加上它的时代也较晚，使我们倾向于认为：它是大熊猫类一个灭绝的旁枝，没有留下现生后代(图 3)。

4. 由于找到了 *Ailuropoda* 和 *Ursavus* 之间的过渡类型，而 *Ursavus* 属于熊科是从未被怀疑过的，因此 *Ailuropoda* 与熊科的亲缘关系应予肯定。至于 *Ailuropoda* 和 *Ailurus* 之间在形态上的相似只能以保留了部分更早期的近祖性状(如前臼齿双根等等)和趋同进化(如前臼齿舌侧的附尖等等)来解释。

5. 大熊猫类现已包含三个属：*Agriarctos*、*Ailurarctos* 和 *Ailuropoda*。它应为熊超科中一个次级分类单元(本文暂用大熊猫科)，它的阶元应在对所有已知熊类研究之后



1) 见邱占祥等, 1987。

图3 大熊猫类地史地理分布及可能的系统关系示意图

Fig. 3 Sketch map showing the distribution of geological history and geography as well as tentative phylogeny of ailuropods

方能解决,这将是另一篇文章的内容。由此看来大熊猫类在中新世晚期已分布于欧洲和亚洲,现今大熊猫分布的局限性应发生在上新世。

6. 大熊猫类的早期代表大多发现于褐煤层中,现在已知的地点至少有 Soblay、Rozsaszentmarton 和禄丰。这表明它们的生活环境应是接近沼泽地带,食物也不会以竹子为主。现生大熊猫的特殊生态环境和狭食性应是相对晚近发生的变化。

禄丰 *Ailurarctos* 化石的数量目前还很少。我们仅仅认识了它的不完整的齿列。对于这种动物的头骨、下颌以至头后骨骼特征的了解,只能寄希望于未来。尽管如此,我们已经可以有理由这么说,人们寻找了近一个世纪的大熊猫的祖先,今天我们终于找到了。

黄万波、韩德芬同志热情为本文作者提供对比标本,沈文龙、代加生同志为本文制作插图,图版照片由杜治同志拍摄,在此一并致谢。

(1988年12月5日收稿)

参 考 文 献

- 朱靖, 1974: 关于大熊猫分类地位的讨论. 动物学报, **20**(2), 174—187.
- 祁国琴, 1984: *Ursavus* 在中国的首次发现——并记禄丰古猿化石产地的其他熊类化石. 人类学学报, **3**(1), 53—61.
- 祁国琴, 1985: 禄丰古猿化石地点食肉目化石的初步整理. 人类学学报, **4**(1), 33—43.
- 邱占祥、阎德发、贾航、王宝忠, 1985: 山东山旺首次发现祖熊牙齿化石. 古脊椎动物学报, **23**(4), 264—275.
- 邱占祥、黄为龙、郭智慧, 1987: 中国的三趾马化石. 中国古生物志, 新丙种第二十五号, 135—147.
- 吴汝康、韩德芬、徐庆华、祁国琴、陆庆伍、潘悦容、陈万勇, 1982: 云南禄丰古猿化石地点再次发现腊玛古猿头骨——1981年发掘报告. 人类学学报, **1**(2), 101—108.
- 裴文中, 1974: 大熊猫发展简史. 动物学报, **20**(2), 188—190.
- 裴文中, 1987: 广西柳城巨猿洞及其他山洞之食肉目、长鼻目和啮齿目化石. 古脊椎动物与古人类研究所集刊, 第十八号, 5—134.
- Davis, D., 1964: The giant panda. *Fieldiana. Zool. Mem.*, No. 3, 1—334.
- Deperet, C. and G. Lluca, 1928: Sur P "*Indarctos arctoides*" et al phylogénie des ursidés. *Bull. Soc. Geol. France* 4 sér., t. 28, 149—160.
- Flynn, L. and G. q. Qi, 1982: Age of the Lufeng, China, hominoid locality. *Nature*, **298**(5976), 746—747.
- Ginsburg, L., 1982: Sur la position systematique du petit panda *Ailurus fulgens* (Carnivora, Mammalia). *Geobios*, mem. special. 6, 247—258.
- Gregory W. K., 1936: On the phylogenetic relationships of the giant panda (*Ailuropoda*) to other arctoid Carnivores. *Amer. Mus. Nov.*, **878**, 1—20.
- Kretzoi, M., 1942: Zwei neue Agriotheriiden aus dem ungarischen Pannon. *Földtani Közlemények*, **72**, 350—353.
- Kretzoi, M., 1982: Funde der *Hipparion*-Faunen im pannon des Karpatenbeckens. *M. All. Földt. Int. Evi. Jel.* 1980-Rol, 385—394.
- Kretzoi, M., 1983: Kontinentalgeschichte und Biostratigraphie im Jungtertiär und Quartär des karpaten-Beckens und ihre Korrelation. *Földt. Közl.*, 1983, Evi 3—4, 230—240.
- Schlosser, M., 1900: Über die Baren und Barenähnlichen Formen des europäischen Tertiärs. *Palaeontogr.*, **46**, 95—147.
- Schlosser, M., 1902: Beiträge zur Kenntniss der Säugetierreste auf den süddeutschen Bohnerzen. *Geol. u. Pall. Abh.*, N. F., **5**(3), 117—258.
- Thenius, E., 1947: *Ursavus ehrenbergi* aus dem Pont von Euboea (Griechenland). *Sitzber. Österr. Akad. Wiss.*, **156**, 225—249.
- Thenius, E., 1979: Die taxonomische und stammesgeschichtliche position des *Bambusbaren* (Carnivora, Mammalia). Gebiss-Analyse und Fossildokumentation. *Anz. math.-naturw. Klasse österr. Akad. Wiss.*, 1979, No. 3, 1—12.
- Viret, J., 1949: Observations complémentaires sur quelques mammifères fossiles de Soblay. *Ecl. Geol. Helv.*, **42**, 469—476.
- Viret, J. and G. Mazenot, 1948: Nouveaux restes de mammifères dans le gisement de lignite pontien de Soblay (Ain). *Ann. Paléont.*, **34**, 3—42.

AILUROPOD FOUND FROM THE LATE MIOCENE DEPOSITS IN LUFENG, YUNNAN

Qiu Zhanxiang Qi Guoqin

(Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica)

Key words Lufeng; Late Miocene; *Ailuropoda*

Summary

As far as its origin and systematic position are concerned, the giant panda (*Ailuropoda melanoleuca*) is one of the most ardently debated animals. The dispute actually started immediately after the animal was first scientifically recognised in 1869, and remains unsettled till now. The major reason for that lies undoubtedly in lacking of fossil evidence. *Indarctos*, *Agriotherium* and *Arctotherium* were sometimes considered closely related to it, but none of them has ever been proved to be ancesto of the giant panda. *Ursavus* has usually been conceived as a group giving rise to the giant panda, however, no reliable links have ever been found so far. The little known *Agriarctos* shows some striking resemblances to the giant panda in morphology, but the fossils are so poor that its real affinity is still obscure. In fact, the earliest fossils that we could attribute to the giant panda group with certainty differ from the latter at most specifically, for instance *Ailuropoda microta* from the early Pleistocene *Gigantopithecus* fauna in South China (see Pei, 1974 & 1987).

A preliminary study of the ursid material collected from the *Lufengpithecus* locality prior to 1981 and discovered later in 1983 was published by one of the present authors (Qi G. q.) in 1984 and in 1985 respectively. Reexamination of all the materials at hand have convinced us that the specimens originally identified as *Ursavus depereti* supposedly represent the earliest record of a true member of ailuropods. This new finding will doubtless play an important role in solving the problems concerning the origin and systematic position of the giant panda in the future.

Brief Description

Carnivora Bowdich, 1821

Ursoidea Hay, 1930

Ailuropodidae Pocock, 1929

Ailurarctos gen. nov.

Type species *Ailurarctos lufengensis* sp. nov.

Diagnostic features same with the type species.

Ailurarctos lufengensis sp. nov.

1984 *Ursavus depereti*: Qi, pp. 53—61; pl.

1985 *Ursavus depereti*: Qi, pp. 33—43.

(Pl. I. 1—6; Fig. 1—2, 1)

Type a left P⁴(V. 6892. 12) from the second layer (see Wu R. K. et al., 1982).

Hypodigm From the second layer: a left P_4 (V. 6892. 13); a left M_3 (V. 6892. 11). From the third layer: a right P^4 with paracone damaged and metastyle completely lost (V. 6892. 1) (originally identified as DP^4); a right M^1 with anterior border broken (V. 6892. 2); a left M^1 with paracone damaged (V. 6892. 3); talon of a right M^2 (V. 6892. 4); a left M^2 (V. 6892. 5); a right M^2 (V. 6892. 6); left P^2 and P^3 (V. 6892. 7) (originally identified as right P_2 and P_4); fragment of left P^4 with only paracone and parastyle still preserved (V. 6892. 9); right M_2 and M_3 (V. 6892. 10). From the fifth layer: right M^2 (V. 6892. 14)

Diagnostic features Morphologically primitive and small-sized animal belonging without doubt to the *Ailuropoda* lineage. The length of its cheek teeth is only about 2/3 that of the recent species. Its premolars are much likethose of *Ailuropoda*, while its molars still principally remain on the level of *Ursavus*. The P^2 is doblerooted, With a minute anterior accessory cusplet. There is no sign to show that it closely imbricates over P^3 . The P^3 is double-rooted and tricuspid. Lingually it is provided with minet cingular cusplets. The P^4 resembles that of *Ailuropoda*. It is three-rooted. The three labial cusps (parastyle, paracone and metastyle) are almost equal in size. They are flat lingually, but strongly convex labially. At the base of its lingual side there are two big cusps: an anterior "protocone" (an outgrowth from cingulum without support by a root of its own) and a posterior "hypocone", which is actually genuine protocone supported by a separate root. Between them a small tubercle is also visible. Labial cingulum is developed. The M^1 is roughly quadrate in form, with its length a little exceeding its width. None of the protoconule and metaconule so characteristic of *Ailuropoda* is reconizable. The protocone and hypocone form a continuous longitudinal ridge, interrupted by a shallow cleft near the hypocone. Cingulum is only weakly developed, the lingual one does not extend posteriorly beyond the hypocone. The M^2 is only a little longer than M^1 . Its talon approximately equals its trigon in size, but differ in shape. The trigon is trapezoid in form, while the talon is rounded. The P^4 is two rooted and tricuspid. The posterior part of its inner side bulges lingually. The trigonid of M_1 is very robust. The anterior edge of the paraconid slopes down gently. The metaconid is a little lower than the protoconid, but rather anteriorly situated, judging from its position relative to the protoconid. The lingual side of M_2 is much higher than its labial side. Its paraconid is still discernible. The M_3 is small and rounded. The crown surface of all the cheek teeth, especially the molars, are covered with deep wrinkles and vermicular ornaments.

Comparison and Comments

The above described fossils are mainly isolated teeth. The arguments in favor of grouping them together into one species are the following: (1) The teeth show great morphological homogeneity, i.e., they all possess features transitional from *Ursavus* to *Ailuropoda*, albeit in different degrees. The most distinctive of these features are the tricuspid premolars and the strongly wrinkled occlusal surfaces of the cheek teeth. The latter feature makes it easy for us to sort these teeth out and separate them from other ursoid teeth of comparable size found from the same locality. In fact, there are two kinds of ursid teeth of similar size at this locality. One is strongly wrinkled, the other is more or less smooth-crowned, which will be studied and published later. (2) All the wrinkled teeth are matchable, as far as their size is concerned. (3) It is most probable that, except one M^2 (V. 6892. 6), the teeth from the third layer might well belong to one and the same individual, since no repetition of any one tooth of the same side occurred here.

1. Comparison with *Ursavus*

Except two species (*U. depereti* and *U. ehrengergi*), which will be discussed later, the typical *Ursavus* differs from *Ailurarctos* clearly. (1) The P^2 , P^3 and P_4 are tricuspid in *Ailurarctos*, while they are principally unicuspid in *Ursavus*. (2) In *Ailurarctos* parastyle of the P^4 is so large that the three labial cusps seem almost equal in size. No real carnassial blade is formed by the paracone and metastyle. The protocone is shifted backward to the position of the hypocone, while anteriorly there is another tubercle taking the position of the shifted protocone. In typical *Ursavus* the parastyle in P^4 is usually lacking, or very small, if there is any. The paracone and metastyle form a carnassial blade as usual. The protocone is only cusp on the lingual side of the tooth and anteriorly situated. (3) In *Ursavus* cingulum is usually well developed, especially on the molars, but in *Ailurarctos* is weak. (4) *Ailurarctos* is characterized by strongly wrinkled occlusal surfaces of the cheek teeth, while in *Ursavus* the enamel wrinkles are weaker, though always present. On the other hand, *Ursavus* and *Ailurarctos* share some common features. (1) They apparently possess full-numbered premolars (in contrast to most of the recent *Ursus*) which are not so closely set or imbricated as in *Ailuropoda*. P^2 , P^3 and P_2 - P_4 are apparently double-rooted (in contrast to most advanced ursines). (2) P^4 has three roots (in contrast to *Ursus*). (3) The morphology and relative size of the molars are about same in both genera. *Ailuropoda* and *Ursus* are quite different in the two respects.

Since the type of *U. depereti* consists of only M_1 and M_2 , we can not say for certain whether the upper teeth from Soblay, France, should really be included in the same species as Viret did (1948 and 1949). What is crucial here are the two P^4 from Soblay (AA 52bis, published in 1948 and AA 96, published in 1949). They are really unusual for a *Ursavus* species. Both have large parastyles and backward shifted and considerably enlarged protocones. The specimen AA 52bis is more advanced in morphology than AA 96. Its protocone is clearly separated into two symmetrical tubercles and the tooth assumes the shape of an isosceles triangle. Based on these characters, Thenius (1979) unequivocally attributed AA 52 bis to the lineage of the giant panda. Careful comparison of the material shows that there are still principal differences between the Lufeng and Soblay specimens, though superficially they are quite similar. (1) Irrespective of the presence of a large parastyle, the P^4 of Soblay remains a typical carnassial tooth with shearing blade formed by the paracone and metastyle which is blade-like rather than cusped. The paracone is preponderant over the other cusps in size and height. (2) The shape of the Soblay P^4 is roughly an isosceles triangle, without the strong backward shifting of the protocone and the widening of the tooth so characteristic of the ailuropods. Whatever the Soblay material might be, it could not be congeneric with the Lufeng specimens.

2. Comparison with *Ailuropoda*

From the foregoing description a suite of common features between *Ailurarctos* and *Ailuropoda* could be observed. (1) P^2 , P^3 and P_4 (probably also P_2 and P_3) of both genera are double-rooted and tricuspid. The cusps of the uppers are convex labially and flat lingually, while the cusps of the lowers are convex lingually, but rather flat labially. (2) The morphology of the P^4 is almost the same for the two genera, radically different from any other members of the ursoids. (3) M^1 and M^2 are heavily wrinkled in both genera and their labial cingulum is almost wanting. (4) The trigonid of the M_1 is particularly robust, with anteriorly shifted me-

taconid in both forms. (5) M_2 and M_3 are similar in relative size and morphology for the two genera. They are strongly wrinkled. The paraconid is still discernible on M_1 .

Ailurarctos differs from *Ailuropoda* in the following points. (1) The premolars are apparently not very tightly set in *Ailurarctos*, neither the imbrication of the P^2 over the P^3 is observed here. (2) The lingual tubercles of the premolars so characteristic of the giant panda are still in their infancy, not very well formed in *Ailurarctos*. (3) The length of the M^1 exceeds its width in *Ailurarctos*, its lingual cingulum does not embrace the whole tooth, neither is it very widened. No protoconule and metaconule are formed in *Ailurarctos*. In *Ailuropoda* the M^1 is wider than long, its lingual cingulum is particularly strong, shelf-like, with well formed proto- and meta-conule. (4) In *Ailuropoda* the M_1 strongly bulges antero-labially and its metaconid is not only anteriorly shifted, but also higher than the protoconid. The bases of the paraconid and metaconid connect with each other, so that the trigonid is closed lingually. All these characters are still not present in *Ailurarctos*. (5) In *Ailuropoda* the trigonid and talonid are clearly separated from each other as demonstrated in both lateral and crown views. It is not so clearly shown in *Ailurarctos*. (6) The M_3 of *Ailurarctos* is proportionally smaller and rounded in shape, while in *Ailuropoda* it is larger and either triangular, or oval in shape.

3. Comparison with *Agriarctos*

This genus was erected by Kretzoi in 1942, based on only lower teeth, P_3 - M_2 (P_4 partly broken). It is true that the premolars of that genus possess characters strongly reminiscent of *Ailuropoda*, such as the double-rooted and tricuspid premolars and the anteriorly shifted metaconid of the M_1 etc. However, the differences between *Agriarctos* and *Ailurarctos* are obvious: (1) *Agriarctos* is much larger in size (see table 1). (2) Its M_2 appears longer relative to its M_1 in comparison with those of *Ailurarctos*. The length index of M^2/M_1 trigonid in *Agriarctos* is 121.7, while that for *Ailurarctos* is only 106.4 (3) Kretzoi mentioned neither the enamel wrinkles on the tooth crowns, nor the cusp morphology of the premolars. If there were strong wrinkles on the occlusal surfaces of the cheek teeth and the labial flatness of individual cusps of the premolars, Kretzoi should not have overlooked them, as they are distinctive and unique in the ursoid group. At any rate, *Agriarctos* should be generically different from the Lufeng form.

The following conclusions could be drawn from the foregoing discussion:

1. The Lufeng specimens described above represent a previously unknown form of ailuropods. It should be separated as an independent genus for which *Ailurarctos* is given in the present paper.

2. What *Ailurarctos* and *Ursavus* share in common are mainly plesiomorphic features relative to most of the advanced members of the ursoids. What *Ailurarctos* differs from *Ursavus* are apomorphic. The common features shared by *Ailurarctos* and *Ailuropoda* are autapomorphic for themselves, absent from all the other members of the ursoids. What *Ailuropoda* differs from *Ailurarctos* are apomorphic for the lineage of the ailuropods. In conclusion, *Ailurarctos* stands phylogenetically between *Ursavus* and *Ailuropoda*.

3. The P^4 from Soblay stands morphologically between those of the typical *Ursavus* and *Ailurarctos*. Judging by its basic pattern and function, the Soblay P^4 is closer to *Ursavus* than to *Ailurarctos*.

4. *Agriarctos* possesses some of the apomorphic features of the ailuropod group. Howe-

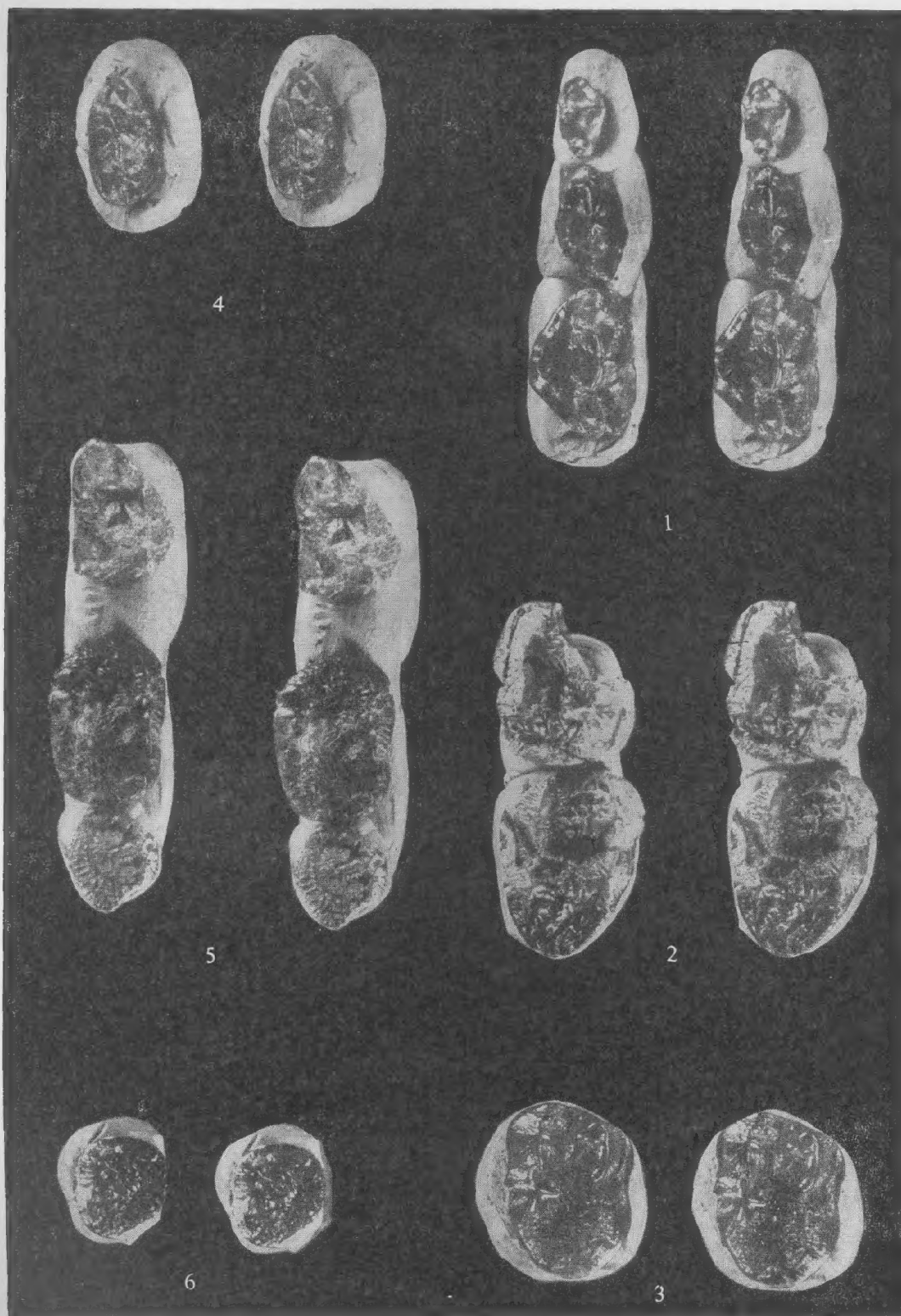
ver, its precociously large size and the lacking of some other ailuropod features tend to show that it might be a sidebranch of the lineage of the giant panda (Fig. 3).

5. Since we have found the missing link (at least in its morphologic sense) between the genuine ursoid, *Ursavus*, and *Ailuropoda*, there is no room for further doubting the ursoid affinity of the giant panda. The similarities between the giant panda and the procyons, especially the small panda, in their premolars should be explained by convergence or parallel evolution.

6. The giant panda is no longer a monotypic taxon. Now this lineage (its taxonomic rank will be dealt with in more details in another paper) consists of 3 genera at least: *Ailuropoda*, *Ailurarctos* and *Agriarctos*. During the late Miocene it was widespread in large territory of Eurasia. Its restriction in distribution should occur mainly during the Pliocene.

7. *Ailurarctos* and *Agriarctos* have been so far mainly known from the lignite deposits (Soblay, Rozsaszentmarton and Lufeng). Their preferable habitat should have been marshland in the subtropical area with variety of plant and animal food resources. Therefore, the extremely strong constriction in distribution and monophagous diet on bamboo of the present-day giant panda should have occurred only recently.

So far we have only a few specimens of *Ailurarctos*. What we know is only some of its cheek teeth. We do not know what its skull, jaw and postcranial skeleton may look like, for which we could do nothing else than to wait in expectation. This notwithstanding, we may now proclaim that after a century's ardent search the ailuropod of the late Miocene which possibly is the ancestor of *Ailuropoda* was eventually found.



禄丰始猫熊 新属新种 (*Ailurarctos lufengensis* gen. et sp. nov.) 立体照片 (stereoscope)
冠面视 (occlusal view) $\times 1.5$

1. 左 P^2 , P^3 (P^2 , P^3 sin.) V. 6892.7, 左 P^4 (P^4 sin.) V. 6892.12; 2. 左 M^1 (M^1 sin.) V. 6892.3, 左 M^2 (M^2 sin.) V. 6892.5; 3. 右 M^2 (M^2 dext.) V. 6892.6; 4. 左 P_4 (P_4 sin.) V. 6892.13; 5. 右 M_1 (M_1 dext.) V. 6892.9, 右 M_2 和 M_3 (M_2 and M_3 dext.) V. 6892.10; 6. 左 M_3 (M_3 sin.) V. 6892.11